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The Silvics of *Castanea dentata* (Marsh.) Borkh., American Chestnut, Fagaceae (Beech Family)

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and Bryan T. Mudder

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Cover Photograph:

Clockwise from top left: American chestnut; the spiny burs of the American chestnut; catkins in full bloom; an open bur, showing the chestnut inside. Photos reprinted with permission from the Southern Research Station Archives.

Preface:

The Woody Plant Seed Manual, originally published as USDA Miscellaneous publication 654 in 1948, was twice revised, most recently in 2008 as Agriculture Handbook 727. These publications were the first attempt to summarize life histories, growth habits, and cultural practices to regenerate tree species in North America. The Woody Plant Seed Manuals included the genus *Castanea*, but provided only brief descriptions of growth habits, blight-resistance breeding, and regeneration practices. "Silvics of Forest Trees of the United States" (USDA Forest Service, Agriculture Handbook 271) was the first document to comprehensively summarize the silvics of tree species, and contained information on 127 species of trees. The handbook did not contain information for the genus *Castanea*. The second publication "Silvics of North America" (USDA Forest Service, Agriculture Handbook 654) also did not contain *Castanea* species. There has been great progress in development of blight-resistant American chestnut progeny, work that was initiated by the U.S. Department of Agriculture and continued by other organizations. Artificial regeneration technology, which will be a requirement for restoration of American chestnut, has also greatly improved, in part through the work of the Institute for Tree Root Biology of the Forest Service, U.S. Department of Agriculture. The Forest Service signed a memorandum of understanding with the American Chestnut Foundation that provides a framework for the Forest Service to assist the Foundation in research and provide lands for plantings of experimental material. Putative blight-resistant progeny was first planted on the national forests in 2009, and planting of chestnut material for reforestation was proposed in 2012 in an Environmental Assessment on the Nantahala National Forest. Guidelines for silvical requirements, regeneration strategies, and management techniques for restoration of this species are needed prior to large-scale planting on public and private lands. This publication is modeled after the "Silvics of North America" in its content with additional sections unique to American chestnut, such as the history of blight-resistance work and current restoration efforts.

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ABSTRACT

This report describes how the American chestnut (*Castanea dentata*) was ecologically extirpated due to an exotic pathogen, the chestnut blight (*Cryphonectria parasitica*), and describes current restoration efforts. The habitat, life history, special uses, and genetics of the American chestnut are detailed. The American chestnut was an important and versatile tree species until its demise from the chestnut blight. Backcross breeding techniques, the use of hypovirulent blight strains, and genetic engineering programs are currently being developed and tested to produce trees resistant to the blight fungus. The first putative blight-resistant trees have been planted and silvicultural techniques to improve competitive ability of chestnut are being tested. American chestnut is a fast-growing species with the ability to persist in shaded conditions and it responds favorably to forest management techniques that limit competition and increase available sunlight. Restoration will require advanced artificial regeneration techniques. The effects of damaging agents other than blight, including root rot caused by *Phytophthora cinnamomi*, Asiatic oak weevil (*Cyrtepistomus castaneus*), the gypsy moth (*Lymantria dispar*), and Asian ambrosia beetles (Coleoptera: Scolytidae) are not well understood but may represent real barriers to restoration.

Keywords: American chestnut, backcross breeding, chestnut blight, exotic species, restoration, silvics, silviculture.

INTRODUCTION

American chestnut [*Castanea dentata* (Marsh.) Borkh.], also called sweet chestnut, was once a widespread and dominant species throughout the deciduous forests of eastern North America (Braun 1950, Russell 1987). American chestnut had the fastest growth and highest abundance in Braun's (1950) oak-chestnut forest region, but the species inhabited nearly all States east of the Mississippi River (fig. 1). The introduction of exotic pathogens, primarily the chestnut blight fungus [*Cryphonectria parasitica* (Murr.) Barr], led to the extirpation of the species as a forest canopy dominant throughout its native range. Root rot caused by *Phytophthora cinnamomi* (Rands) also contributed to the demise of *Castanea* species growing in lowland or riparian areas (Russell 1987). The effects of these exotic pests resulted in the current listing of American chestnut as a species of special concern in Maine and Tennessee and as an endangered species in Kentucky and Michigan (USDA Plants Database 2012). The Committee on the Status of Endangered Wildlife in Canada listed American chestnut as threatened in 1987 and changed the status to endangered in 2004 (Tindall and others 2004).

American chestnut was one of the most valued and beloved eastern hardwood species due to its use as a timber tree, its abundant nut production, and its secondary wood products (Emerson 1846, Zeigler 1920). American chestnut grew straight and tall, reaching up to 5 feet in diameter and 120 feet in height, and the species could live for several hundred years (Buttrick 1925). It was among the most versatile trees on the continent, historically used for construction lumber, shingles, fence posts and rails, poles, paneling, trim, furniture, and firewood (Ashe 1911, Detwiler 1915, Emerson 1846, Zeigler 1920). The wood was important in the charcoal iron furnace industry in the northern hardwoods region (Emerson 1846) and is highly resistant to decay because of its high tannin content. Extracted tannins from chestnut once drove the leather tanning industry in the Northeastern United States (Youngs 2000). American chestnut produced copious amounts of flavorful nuts that were consumed by humans and wildlife (Frothingham 1912, Hawley and Hawes 1925, Hepting 1974, Smith 2000, Zeigler 1920).

At its greatest distribution, American chestnut constituted up to one-fourth to one-half of the canopy trees in its native range, and because of its desirable characteristics, it was widely planted in orchards and along streets, roadsides, and fencerows for shade, windbreaks, nut production, and aesthetics (Burnham 1988, Emerson 1846, Emerson and Weed 1908, Russell 1987). In the early 1900s, American chestnut made up more than 25 percent of all timber cut in the Southern Appalachians, was the most valuable tree in southern New England, and constituted almost half of the timber cut in Connecticut (Frothingham 1912, Hawley and Hawes 1925, Hepting 1974). The species was described as "one of the most promising trees for forest management" in Tennessee (Ashe 1911) and "one of the most promising trees for forestry planting" at the onset of professional forestry in the United States (Emerson and Weed 1908).

The demise of American chestnut followed the introduction of two exotic fungi and is regarded as the most tragic ecological event in the post-glacial history of eastern North American forests (Jacobs 2007). Root rot caused by *Phytophthora cinnamomi* was found to affect American chestnut as early as 1824, with the greatest impact on trees in riparian areas, heavy clay soils, and low-lying valleys (Anagnostakis 2002, Crandall and others 1945). The disease was initially most damaging in the Piedmont and Coastal Plain regions but was also noted in mountainous areas, moving from low to progressively higher elevations (Anagnostakis 2002, Crandall and others 1945, Russell 1987). Unlike the chestnut blight, trees infected with *Phytophthora* root rot cannot maintain above-ground stems for long before death.

The chestnut blight is an aggressive diffuse canker disease that was introduced along with imported *Castanea* spp. seedlings from Asia (Anagnostakis 1987). The disease was first detected in 1904 at the Bronx Zoological Park in New York City (Merkel, 1905, Roane and others 1986); by 1950, the disease had spread throughout the range of American chestnut, and by 1960 it had killed an estimated 4 billion trees and essentially extirpated the species as a canopy tree (Anagnostakis 1987, Hepting 1974, McCormick and Platt 1980). However, American chestnut is still a common component of eastern deciduous forests, persisting as understory sprouts that originated from blight-killed trees and saplings (Russell 1987, Stephenson and others 1991). The cycle of sprouting, infection, and dieback continues, with sprouts generally not exceeding small tree size and rarely growing to reproductive maturity (Paillet 1984, 2002).

Recent advancements in the production of putatively blight-resistant American chestnut trees indicate that restoration may be imminent (Clark and others 2011, 2012a). Because of the unique history of this species, relatively little is known about its ecology and life history. The objective of this technical report is to synthesize the current understanding of the silvics of American chestnut in order to facilitate current and future restoration efforts.

HABITAT

Native Range

American chestnut reached its maximum distribution in the United States about 2000 years before present, when the species established in New England forests for the first time (Davis 1983, Paillet 2002). By the late 19th century, the American chestnut range extended from central Mississippi and Alabama through the Appalachian region and into New Hampshire, Vermont, and Maine; the range extended west into Ohio and Indiana and into portions of southern Ontario, covering an area greater than 309,000 square miles (Braun 1950, Hawley and Hawes 1925, Russell 1987, Woods 1953) (fig. 1). Other reports suggest the possibility of a more extensive range, for example, Woods (1953) found chestnut far south in the Gulf Coastal Plain, occurring with longleaf pine (*Pinus palustris* Mill.) in southern Alabama, Florida, and Louisiana.

According to Braun (1950), the most concentrated abundance of American chestnut in its native range falls within the Oak-Chestnut Forest and the Mixed Mesophytic Forest regions. In the Oak-Chestnut Forest region, American chestnut was often the dominant tree species, comprising an estimated 25 percent of hardwood forests (Burnham 1988). In portions of the Appalachian Mountains, chestnut was thought to have made up 40 to 50 percent of the forest canopy (Braun 1950), and in the Southern Appalachian Mountains, it could occasionally form pure stands (Buttrick 1915). Saucier (1973) reported that the species made up 15 billion board feet or 25 percent of the total timber volume in the Southern Appalachian Mountains. Chestnut trees comprised 50 percent of the timber on the mountainous ridges of western Maryland, dominated 26 to 36 percent of the slope forests of Maryland, and were estimated to hold 3.75 billion board feet of timber in the Blue Ridge Mountains of North Carolina (Buttrick 1915). Chestnut-dominated stands formed 50 percent of second growth forests in New Jersey, Pennsylvania, Connecticut, and southern New England (Frothingham 1912, Hough 1878, Russell 1987). Most of these species composition estimates were made after the disturbances associated with European settlement, such as grazing, land-clearing for agriculture, uncontrolled wildfires, and indiscriminant logging (Abrams 1992, 1996). Chestnut regeneration probably increased following repeated disturbance due to its ability to prolifically sprout and occupy abandoned agriculture fields (Matoon 1909, Paillet 2002); therefore, historical species composition estimates may overestimate chestnut abundance prior to European settlement. Nevertheless, chestnut was perhaps the most widespread and abundant species in the Eastern United States since the last glaciation, with the highest concentration of American chestnut in the Southern Appalachian Mountains.

Climate

In the native range of American chestnut, mean annual precipitation varies from about 32 inches in western New York and southern Ontario to about 80 inches in the Southern Appalachian Mountains; however, annual precipitation for the majority of the native range is between 40 inches and 48 inches. Annual snowfall ranges from only trace amounts in the Southern United States to 100 inches

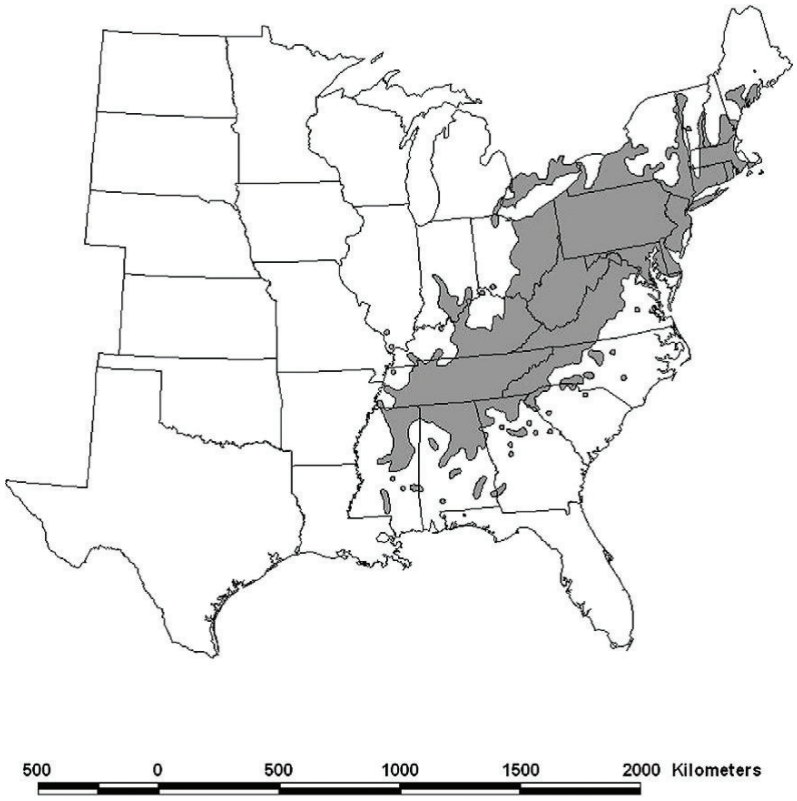

Figure 1—Original native range of American chestnut in eastern North America, as adapted from Little (1977) by Jacobs (2007)

or more in the Northern United States and in Canada. Mean annual temperature is about 40 °F in the northern part of the range and 60 °F in the extreme southern part. The frost-free period averages 100 days in the Northern United States and 240 days in the Southern United States.

Although American chestnut is believed to be the most cold-hardy species of the *Castanea* genus (Huang 1998), it is prone to frost damage (Gurney and others 2011, Paillet 1988, Parker and others 1993, Zon 1904), which may have affected its northern range and upper altitudinal limits (Russell 1987). Zon (1904) noted a lack of American chestnut in the bottoms of ravines and valleys because frosts commonly occur on wet, protected soils. Braun (1950) reported American chestnut occurring at elevations of 1,300 to 4,500 feet in the Southern Appalachian Mountains, with the possibility of occurrence at higher elevations of 4,000 to 5,500 feet on southern exposures. In North Carolina, Buttrick (1925) found American chestnut growing between elevations of 500 feet and 5,500 feet. American chestnut grew at lower elevations in northern latitudes, occurring at elevations < 3,000 feet in the Catskill Mountains (Russell 1987) and at elevations < 400 feet in New Hampshire (Hough 1878).

Only one study has examined climate-tree growth relationships of American chestnut (McEwan and others 2006). The relationships between American chestnut growth and climate were similar to those of other hardwoods, with increasing growth associated with increasing precipitation and decreasing Palmer Drought Severity Index values during the growing season. However, American chestnut growth had strong positive relationships with August precipitation of the current year and strong negative relationships with August temperature of the previous year, suggesting it may be slightly more sensitive to late growing season climate than other hardwoods.

Soils and Topography

American chestnut naturally occurs on a wide range of soil and topographic conditions but is most commonly associated with well-drained, subxeric to mesic soils that often occur on sand plains and dry ridges (Abrams and Ruffner 1995, McEwan and others 2005, Paillet 2002, Russell 1987, Stephenson and others 1991). American chestnut is believed to grow poorly in very wet or very dry soils, and rarely grows in areas with high pH or on limestone-derived soils (Braun 1950; Frothingham 1912;

Paillet 1988, 2002; Russell 1987). Within a soil pH range of 3.3 to 5.5, chestnuts were more abundant at the higher end of the range (pH of 4-5) in a study conducted in southwestern Virginia (Burke 2011). A recent survey of surviving trees in Canada found that American chestnut was most likely to occur in deciduous forest habitats with high canopy cover (> 50 percent), gentle slopes (0 to 10 percent) and acidic (pH 4–6), sandy (> 75 percent) soils (Tindall and others 2004). In the southern portion of the range, the occurrence of American chestnut on northern side slopes increased with topographic relief, and the species was negatively associated with the more calcium rich soils and lower relief of the Coastal Plain region (Black and others 2002). The presence of American chestnut often indicates acidic soils derived from gneiss, metamorphosed sandstone, and sandstone that is deficient in lime and potash (Frothingham and others 1926). A recent study also reported that American chestnut height growth was negatively correlated with pH (Tindall and others 2004).

Although the Society of American Foresters included American chestnut as a characteristic tree in the cove hardwood forest type (Frothingham and others 1926), it is not clear to what extent American chestnut occurred in cove or ravine sites. Frothingham (1912) and Braun (1950) indicate that chestnut was not commonly found on moist cove sites, but Ashe (1911) and Buttrick (1925) suggest the opposite. Ashe (1911) reports that American chestnut grew best in rich, deep coves in Tennessee, and Buttrick (1925) observed that American chestnut in cove forests produced the best timber. More recent evidence supports that American chestnut contributed substantially to the canopy of ravine and cove sites in the Cumberland Plateau and Southern Appalachian Mountains, e.g., more survivors were found in ravine sites than on ridge-top sites (Hinkle 1989), and chestnut potentially represented 25 to 40 percent of the basal area in pre-blight riparian stands (Vandermast and Van Lear 2002). Additionally, McCament and McCarthy (2005) observed that first-year seedling growth was negatively correlated with the proportion of sand in the soil, suggesting the superior suitability of finer textured soils in cove sites for chestnut growth.

The dominance of American chestnut may have affected nutrient cycling and soil chemistry (Ellison and others 2005), although a replicated study examining chestnut leaf litter effects on soil biogeochemical properties has not been conducted. One descriptive study found that most soil nutrients on sandy loam soils were higher under chestnut canopies compared to areas without chestnut (Rhoades 2007). As soil texture became finer, this effect disappeared, suggesting that effects of American chestnut leaf litter on soil chemistry are dependent on soil texture.

Soil nutrient requirements— American chestnut grows and remains competitive over a wide range of soil nutrient regimes. It was frequently found on relatively nutrient deficient to moderately fertile soils (Russell 1987, Zon 1904). Although American chestnut tolerates relatively low soil nutrient levels, it responds well to increasing soil nutrients. Latham (1992) demonstrated improved seedling growth with increasing soil nutrient availability in a greenhouse study. Furthermore, positive growth and/or biomass response reported for American chestnut seedlings has been associated with increasing availability of magnesium (leaf mass and area, root mass), potassium (diameter, specific leaf area) (McCament and McCarthy 2005), and nitrogen (stem, root, leaf parameters) (McCament and McCarthy 2005, Rieske and others 2003).

Soil moisture regime— American chestnut is a relatively drought tolerant species, as suggested by its historical dominance on upland sites with well-drained, sandy soils. During an early-season drought in a hardwood forest in Pennsylvania, American chestnut saplings maintained higher leaf water potential than several associated oak (*Quercus*) species that are known for their drought tolerance (Abrams and others 1990). Recently, Bauerle and others (2006) reported high water use efficiency of American chestnut seedlings exposed to drought compared to published reports of co-occurring hardwood species. However, American chestnut is reported to require more moisture than associated oaks, including black oak (*Quercus velutina* Lam.), scarlet oak (*Quercus coccinea* Münchh.), and chestnut oak (*Quercus prinus* L.) (Frothingham 1912). Alternatively, American chestnut growth was less related to drought during the growing season of the previous year compared to other hardwoods in the same stand (McEwan and others 2006). The reported dominance of American chestnut in cove forest sites, as well as on well-drained upland sites, suggests that the species can compete across a wide range of soil moisture regimes (Ashe 1911, Buttrick 1925, Vandermast and Van Lear 2002).

Associated Forest Cover

American chestnut is capable of forming pure stands, but historical reports suggest that pure stands were rare (Buttrick 1915, Frothingham 1912, Zon 1904). In Braun's (1950) classification of forest communities, American chestnut was the dominant tree species in the Oak-Chestnut Forest region (Frothingham and others 1926, Paillet 2002, Russell 1987). The Oak-Chestnut Forest region included five sections: (1) the Southern Appalachian section; (2) the Northern Blue Ridge section; (3) the Ridge and Valley section; (4) the Piedmont section; and (5) the Glaciated section.

Common associates of American chestnut in the Southern Appalachian Mountains included buckeyes (*Aesculus* spp.), basswood (*Tilia americana* L.), yellow poplar (*Liriodendron tulipifera* L.), eastern hemlock [*Tsuga canadensis* (L.) Carrière], white pine (*Pinus strobus* L.), pitch pine (*Pinus rigida* Mill.), table mountain pine (*Pinus pungens* Lamb.), northern red oak (*Quercus rubra* L.), white oak (*Q. alba* L.), black oak, scarlet oak, and chestnut oak. The canopy trees were often associated with an ericaceous shrub layer consisting of *Rhododendron* spp., *Azalea* spp., *Kalmia* spp., *Vaccinium* spp., *Leucothoe* spp., *Menziesia* spp., and others depending on geographic region and elevation (Braun 1950, Russell 1987, Vandermast and Van Lear 2002).

In the Glaciated section, American chestnut was commonly associated with red oak, scarlet oak, white oak, chestnut oak, pignut hickory (*Carya glabra* Mill. Sweet), American beech (*Fagus grandifolia* Ehrh.), and yellow poplar with an ericaceous understory (Braun 1950). In the Catskill Mountains of New York, American chestnut was observed in mixed deciduous forests along with American beech, northern red oak, butternut (*Juglans cinerea* L.), sugar maple (*Acer saccharum* Marsh.), and an understory of *Rhododendron* spp., *Kalmia* spp., and other ericaceous shrubs (Russell 1987).

In the Northern Blue Ridge section, American chestnut was commonly associated with yellow poplar, northern red oak, white oak, chestnut oak, sugar maple, eastern hemlock, and basswood, with *Rhododendron* species, mountain laurel (*Kalmia latifolia* L.), and blueberry (*Vaccinium* spp.) as common understory species (Braun 1950).

American chestnut associates in the Ridge and Valley section included northern red oak, scarlet oak, white oak, chestnut oak, white pine, eastern hemlock, and yellow poplar, with an ericaceous understory similar to that already mentioned (Braun 1950).

In the Piedmont section, chestnut is being replaced by white oak, black oak, northern red oak, post oak (*Quercus stellata* Wangenh.), blackjack oak (*Quercus marilandica* Münchh.), chestnut oak, yellow poplar, and American beech, with an understory of dogwoods (*Cornus* spp.) and hickories (*Carya* spp.) mixed with the heath layer (Braun 1950).

American chestnut was also one of the dominant trees in the Mixed Mesophytic Forest region that encompasses the Cumberland Mountains, Cumberland and Allegheny Plateau, and Allegheny Mountain sections. It was commonly associated with American beech, yellow poplar, basswood, sugar maple, yellow buckeye (*Aesculus flava* Aiton), northern red oak, white oak, and eastern hemlock (Braun 1950). American chestnut was the most dominant species in the Allegheny Mountain section, where it was commonly associated with northern red oak, white oak, black oak, scarlet oak, yellow poplar, hickories, black gum (*Nyssa sylvatica* Marsh.), black birch (*Betula lenta* L.), basswood, sugar maple, and beech.

Associated forest cover of American chestnut is highly dependent on disturbance history. The composition of many forests once containing a major component of chestnut are succeeding from an oak-hickory dominated association (Keever 1953, McCormick and Platt 1980) to one dominated by maple or shade-intolerant species (Abrams 1998, Lorimer 1984). In a recent survey of surviving American chestnut sprouts and trees in the Coastal Plain, Highland Rim, and Cumberland Plateau regions of Kentucky and Tennessee, 66 percent of the sampled American chestnut trees ($n > 2{,}000$) occurred within 49 feet of red maple trees (Schibig and others 2005). Oak species were recorded in < 30 percent of plots that surrounded American chestnut. Red maple (*Acer rubrum*, L.) was historically not a major component of these forest ecosystems (Braun 1950), but it has become more common with changes in disturbance dynamics (Abrams 1998, Nowacki and Abrams 2008).

LIFE HISTORY

Reproduction and Early Growth

Flowering and fruiting— American chestnuts are monoecious, with male and female reproductive parts on the same tree (Brown and Kirkman 1990, Zon 1904). Flowers are staminate catkins that are borne on a central axis 5 to 10 inches long and are produced in clusters from the axils of leaves. Flowers appear from late May to June, after frosts have passed (Brown and Kirkman 1990; Zon 1904). Weak lower lateral shoots consist of all male flowers, while stronger upper vertical shoots have male flowers on upper shoots and female flowers on lower shoots. American chestnut pollen is not as abundantly dispersed as that of many other wind-pollinated tree species and often requires another tree within 328 feet to reproduce (Paillet 2002, Russell 1987). Pollen is not dispersed until after full leaf development has occurred, and only pollen escaping above the forest canopy can be dispersed for long distances (Russell 1987). The fruit of American chestnut, maturing between September and October, is a brown edible nut with a sweet taste (Brown and Kirkman 1990), and the species was sometimes referred to as sweet chestnut due to its flavorful nut (Van Fleet 1914). The nut develops within a round prickly green bur that produces two to three nuts in each bur (Saucier 1973, Zon 1904).

Seed production and dissemination— American chestnut is a prolific seed producer and one of the most fruitful among all American nut-producing species. It is able to produce fruit as early as age 4 when open-grown, or at about 8 to 20 years old when competing with other trees in the forest (Paillet and Rutter 1989). Reproduction starts earlier and yields more nuts in trees reproduced by coppice than in trees regenerated from seed. A mature tree can produce 1.5 to 3 bushels or up to 6,000 nuts per year (Paillet and Rutter 1989), and unlike other nut producers that display variable masting behavior, such as white oak, American chestnut is a dependable seed producer every year. The dependable seed production is probably due to its late flowering that avoids frost damage. The fruit typically drops with the first frosts of autumn, which opens the bur, and the seeds germinate the following spring (Zon 1904).

Chestnuts were historically an important food for wildlife, to the point that seed predation combined with insect damage limited the success of reproduction from seed (Detwiller 1915, Hawley and Hawes 1925). Chestnut provided a more stable and more abundant source of mast for wildlife than oaks, hickory, and beech species (Diamond and others 2000). Additionally, the nuts were extensively harvested by humans as a source of food and income (Hawley and Hawes 1925, Hepting 1974, Saucier 1973). As a result of the high demand for chestnuts by wildlife and humans, Paillet and Rutter (1989) report that only 1 to 5 viable seeds germinated into seedlings that survived for more than 1 year. When seeds were not consumed by animals or damaged by insects, chestnuts generally had high germinate success, with 60 to 70 percent germination observed in the field (McCament and McCarthy 2005) and > 90 percent germination in the greenhouse (Wang and others 2006) and in commercial tree nurseries (Clark and others 2012b.).

Like many other large-seeded trees, American chestnut seeds were dispersed by wildlife species that included birds and squirrels (*Sciurus* spp.). The American crow (*Corvus brachyrhynchos*), blue jay (*Cyanocitta cristata*), wild turkey (*Meleagus gallaparo silvestris*), ruffed grouse (*Bonasa umbellus*) and passenger pigeon (*Ectopistes migratorius*) were major dispersers of large fruit and probably important for chestnut dispersal (Russell 1987, Webb 1986). Large mammals such as white-tailed deer (*Odocoileus virginianus*) or black bear (*Ursus americanus*) may have also played an important role in the dispersal of American chestnut, as the bur is thought to be an evolutionary adaptation for hitchhiking on mammalian fur.

Seedling development— Natural regeneration from seeds was probably rare in pre-blight years. The nuts were damaged by insects (Detlefson and Ruth 1922, Russell 1987) and highly utilized as a wildlife food source (Detwiler 1915). Small seedlings were easily killed by fire or frosts (Ashe 1911).

Artificial regeneration of nursery-grown seedlings will be a crucial component of restoration. Once sufficient lines of blight-resistant seedlings are developed and tested, they can be planted, cross-pollinate with one another, and sexually reproduce. However, restoration of this species will probably always involve planting, due to the loss of seedlings from nut predation and high seedling mortality.

Seedlings grow rapidly in the greenhouse or in the field as nursery-grown bare-root seedlings or direct-seeded regeneration. Artificially regenerated chestnuts grow best under moderate- to high-light conditions but are capable of surviving under low-light conditions. Seedlings averaged 3 to 4 feet in height and 0.5 to 0.6 inches in diameter at the root collar after 1 year in a commercial tree nursery after receiving steady applications of fertilizer throughout the growing season (Clark and others 2009, 2011, 2012b). Large, nursery-grown, seedlings generally outperform smaller seedlings due to the ability of the larger seedlings to reach heights above browse and natural woody competitors (Clark and others 2011). After 1 year in the field, nursery-grown seedlings that were not browsed by deer averaged 7 inches in height growth and had 80-93 percent survival if not affected by root rot caused by *Phytophthora cinnamomi* (Clark and others 2012a). Larger nursery seedlings appear to allocate more growth to the root system after being field-planted than do smaller nursery seedlings and, consequently, are better suited to resist transplant shock (Clark and others 2009, 2011). Three growing seasons after planting nursery-grown seedlings in the field, seedlings averaged 0.91 inches and 0.94 inches in root collar diameter and 63 inches and 91 inches in height, respectively, when grown in 100 percent and 34 percent full sunlight (Anagnostakis 2007). Early results indicate that trees bred for blight-resistance are similar to American chestnut but differ from Chinese chestnut with respect to height growth rates (Clark and others 2011, 2012a).

Direct-seeding American chestnuts may provide an alternative to out-planting nursery-grown seedlings on certain sites but will require intensive management to avoid predation by mammals and to maintain the competitive status of the seedlings. Two-year survival from direct seeding ranged from 40 to 50 percent in a field study in Ohio (McCament and McCarthy 2005). After 2 years of growth under partial forest shade (~ 25 percent open sky), direct-seeded seedlings averaged ~ 0.23 inches in root collar diameter and ~ 14 inches in height (McCament and McCarthy 2005). Under full sunlight, seedlings grown from seed in the greenhouse averaged ~ 0.20 inches in root collar diameter and ~ 12 inches in height after one growing

season; seedlings allocated < 30 percent of the total carbon gain to below-ground biomass, compared to > 65 percent allocation to below-ground biomass for white oak (Wang and others 2006). Latham (1992) reported that first-year American chestnut seedlings grew faster in height, leaf area, and total dry mass under different levels of nutrients when compared to co-occurring species, including mockernut hickory [*Carya alba* (L.) Nutt], northern red oak, American beech, blackgum (*Nyssa sylvatica*) and tulip poplar. However, root-to-shoot ratios were among the lowest for American chestnut (Latham 1992), further indicating that early growth is allocated to above-ground biomass rather than root systems.

Vegetative reproduction— American chestnut is a tenacious sprouter, and its ability to repeatedly produce large numbers of fast-growing sprouts following dieback is largely responsible for its persistence in forests today (Hawley and Hawes 1925). Natural sprouts will probably exist in the forest for years to come, but American chestnut will never again be a significant component of the forest canopy without the introduction of blight-resistant seedlings. Sprouts that live long enough to bear fruit are valuable because they can be used to maintain genetic diversity in breeding programs (Pierson and others 2007) and for in situ tests of blight resistance and hypovirulence (Anagnostakis 2001, Griffin and others 1983).

Frothingham (1912) attributes the "prodigious sprouting capacity" and rapid growth of American chestnut as reasons for the species' great abundance in second-growth Connecticut forests prior to the blight. Prolific sprouting is considered an adaptation for long-term survival in the forest understory (Paillet 1984, 2002). Sprouts of American chestnut arise from dormant buds that may exist for several years before developing into a shoot or from adventitious buds that develop following localized stimulation (Mattoon 1909, Paillet 1984). Chestnut rarely develops stool sprouts because the narrow region of sprouting is generally in contact with the ground or just above it. However, low-cut stumps tend to have sprouts of deeper origin and show a tendency to develop new lateral roots (Mattoon 1909). In a study by Zon (1904), chestnut was found sprouting principally from the root collar, and the best sprouts were found on low stumps.

Although American chestnut is reportedly able to produce sprouts from trees up to 170 years old, the optimum age for sprouting is probably < 75 years (Mattoon 1909, Zon 1904). Mattoon (1909) observed that old stumps produce a full thicket of short, spindling sprouts, while young stumps generate a smaller number of tall, stout sprouts. Paillet (1984) characterized the growth form of sprouting American chestnuts in the northeast and found it to be highly variable. Sprouts developed a shrub-like form when grown in the shade but expressed strong apical dominance and rapid growth when released, suggesting a growth strategy well suited to periodic disturbance and release from the canopy. The most vigorous sprouts are produced at periods of maximum growth in height, which occurs within the first decade in coppice trees (Zon 1904) or 20-30 years in stands regenerated from seedlings (Mattoon 1909).

Coppice trees grow faster than trees regenerated from seed during the first 20 years. Because of their fast initial growth, sprouts reach their maximum average height growth rate during the first decade of growth. Mattoon (1909) observed rapid height growth (4 to 7 feet per year) in the first year but then a sharp decrease (2 to 3 feet per year) in the second and third year. Diameter growth continues well after height growth has decreased (Zon 1904). An increase of nearly 1 inch per year in diameter during the first 8-15 years has been observed under the most favorable conditions (Mattoon 1909).

Dormant season cutting favors the production and growth of sprouts. Mattoon (1909) reportes that midwinter cutting produced sprouts of superior first-year growth when compared to May cutting: 6.2 feet versus 3.5 feet in height and 0.42 inches versus 0.23 inches in diameter, respectively. Early recommendations for cutting include: (1) late fall to early spring cutting to avoid production of weak sprouts too tender to stand frost; (2) cutting stumps low and at a slight angle to allow water runoff; and (3) avoiding damage to bark which may in turn damage buds (Frothingham 1912, Zon 1904).

Chestnut sprouts remain an important component of understory vegetation throughout the species' former range (Paillet 1984). However, Paillet (1984, 1988, 2002) concluded that a majority of these sprouts were not associated with canopy trees killed by the blight but instead probably originated from former seedlings that had been through several cycles of fungal infection and resprouting or were from sprouts developed from canopy trees cut before the blight. Griffin and others (1991) observed that sprouts generally did not exceed 2 inches in diameter at breast height (d.b.h.) 10 years after sprouting in a clearcut before dying back from blight. Paillet (1984) alludes to sprouting as a reproductive strategy for chestnuts awaiting a crown opening because sprouts are capable of rapid transformation from small, suppressed stems to straight, vigorous saplings in a short time. Suppressed chestnut stems that have escaped blight for several decades develop a form with a single stem or a single stem with at least one weak secondary stem (Paillet 2002).

Sapling and Pole Stages to Maturity

Growth and yield—Early studies indicate that American chestnut is highly competitive and fast-growing during early growth (Ashe 1911, Graves 1905, Zon 1904). These historical observations have been confirmed in recent studies. Jacobs and Severeid (2004) reported that juvenile plantation growth of American chestnut on blight-free sites in Wisconsin greatly exceeded that of interplanted black walnut (*Juglans nigra* L.) or northern red oak. In a recent study (Jacobs and others 2009), American chestnut averaged 3.5 inches in d.b.h. and 28.5 feet in height 8 years after planting and 10 inches d.b.h. and 45 feet in height after 19 years. Paillet and Rutter (1989) described the ability of introduced American chestnut to rapidly out-compete and eventually replace native tree species (e.g., *Quercus* spp., *Carya* spp.) as the dominant canopy tree in a Wisconsin forest. Studying American chestnut development in this same forest, McEwan and others (2006) documented that the growth of American chestnut trees released from the forest canopy following a logging event exceeded that of associated hardwoods by nearly a factor of two.

The timber yield of American chestnut varied greatly depending on the dominance of American chestnut in the stand. Buttrick (1925) estimated that pure stands of American chestnut could yield as high as 20,000 board feet per acre and yielded approximately 20 to 30 billion board feet in the United States (Buttrick 1915). In mixed stands, Buttrick (1925) reported yield at an average of 4,000 board feet per acre with an estimated maximum of 10,000 board feet per acre for cove forests. The yield on slopes was estimated at 2,000 to 3,000 board feet per acre and that on ridges was reported at 1,500 board feet per acre. A study in Tennessee reported average annual yield of approximately 500 board feet per acre per year over a 60-year rotation (Holmes 1925). In a recent study, Jacobs and others (2009) reported that biomass accumulation reached almost 80 tons per acre in a 19-year-old plantation.

Rooting habit—Little is known about the rooting habit of American chestnut, and inconsistent descriptions were found in the literature. Some describe American chestnut as having a shallow root system (Buttrick and Holmes 1913, Paillet 2002), yet others report that American chestnut is a deep-rooted species with a tap root similar to oak and lower lateral roots that spread up to 3.3 feet deep in the soil (Smith 2000, Zon 1904). Chestnut tap roots may divide into many vertical roots that extend 3 to 6 feet, each of which may develop many lateral roots (Smith 2000). Studies of American chestnut growing in the nursery indicate that chestnut seedlings have a main tap root with many lateral roots, similar to that of oak species (Clark and others 2009), and the number of lateral roots is positively correlated to both height and root collar diameter (Clark and others 2009, 2012b).

Reaction to competition—Although American chestnut has been shown to outgrow competing hardwood species, the presence of abundant competition reduces chestnut growth (Griffin and others 1991). Insight into the competitive nature of American chestnut can be traced back to historical pollen records. Range expansion of American chestnut during the Holocene from glacial refugia was the most recent of wind-pollinated trees (Paillet 1982, 2002, Russell 1987), and its rapid expansion to canopy dominance implicates American chestnut as an exceptionally competitive species.

The shade tolerance of American chestnut is still under debate (Joesting and others 2009, Wang and others 2006). Early observations suggest that American chestnut is relatively intolerant (Frothingham 1912, Hawley and Hawes 1925) to moderately tolerant (Zon 1904) of shade. Recent studies have classified American chestnut as either shade tolerant (Wang and others 2006) or intermediately shade tolerant (Joesting and others 2009). In the first study to use contemporary instrumentation on American chestnut, Wang and others (2006) suggested that American chestnut is shade tolerant based on physiological characteristics that include low light compensation and saturation points measured in a greenhouse study, and these results were later confirmed in field studies (Joesting and others 2007, 2009).

The shade tolerance of American chestnut is supported by other studies on morphology, survival, and growth under canopy shade. Paillet (1982) found that chestnut can survive in deep shade under the canopy for up to three decades and is more shade tolerant than co-occurring sub-canopy species. When growing in a light-limited environment, American chestnut increases its specific leaf area (Joesting and others 2009, King 2003, McCament and McCarthy 2005, Wang and others 2006) and develops canopy architecture that is optimal for harvesting light (Paillet 1982). Anagnostakis (2007) found that seedlings growing in the field under 63 percent shade cloth had more above-ground mass than those growing in full sunlight after three growing seasons. However, the shade tolerance of artificially regenerated seedlings may be different than those growing as sprouts. Seedlings planted as bare-root nursery stock may not be able to withstand shade due to the relatively small carbohydrate reserves stored in the newly developed root system, compared to a native sprout with an older, well-established root system.

Joesting and others (2009) reported that natural chestnut seedlings and saplings can subsist in the understory for

many years, have a low dark respiration rate, high quantum efficiency, low N percent, low leaf mass per area, and high light-induced morphological plasticity, all of which are characteristic of a shade tolerant species. However, Joesting and others (2009) classified the shade tolerance of American chestnut as intermediate based on their finding that American chestnut has a maximum photosynthesis rate comparable to shade intolerant species. To justify their classification, Joesting and others (2009) also cited previous observations that American chestnut can rapidly assume a canopy position following the creation of canopy openings (Jacobs and Severeid 2004, McEwan and others 2006) and that seedlings respond well to increasing light both in greenhouse (Latham 1992, Wang and others 2006) and field conditions (Boring and others 1981, Griffin 1989, McCament and McCarthy 2005, Tindall and others 2004). However, we argue that the ability to fill gaps in the canopy does not confer shade intolerance to a tree species. In fact, this strategy is commonly used by many shade tolerant species, e.g., red maple.

Considering all the published evidence, we maintain that American chestnut should be classified as shade-tolerant. Indeed, the continuous survival of chestnut sprouts from blight-killed advanced regeneration in former American chestnut forests (Paillet 2002) is the best testament of its shade tolerance. Its strong ability to survive for prolonged periods in deep canopy shade (Paillet 1982), coupled with its ability to grow well under partial shade (Anagnostakis 2007), suggests that chestnut maintains its presence in the understory in anticipation of disturbance events (Jacobs 2007), with a strategy similar to that of other *Fagaceae* species, e.g., oaks. The rapid height growth of American chestnut following release or after planting in full sun (Billo 1998; Clark and others 2009, 2012a; McEwan and others 2006; Paillet 1982, 2002; Paillet and Rutter 1989) distinguishes American chestnut from co-occurring intermediately shade tolerant species such as oaks (Paillet 2002).

Competition can also affect blight development on American chestnut seedlings. Field tests indicate that blight may be more common on sprouts growing in open or clear-cut sites compared to sprouts growing in the understory of mature forests (Griffin 1989, Griffin and Elkins 1986, Reynolds and Burke 2011). However, after blight has infected the site, surviving trees appear to better withstand the blight if released from competition. The causal factor may be related to hypovirulence, which may be more prevalent if competition is controlled and chestnut stems are allowed to take a dominant canopy position (Griffin 1989). Therefore, mesic sites may offer the best opportunity for biocontrol of the fungus through hypovirulence (Griffin 1992), but such sites will also have the most need for competition control.

Allelopathy—Leachate from American chestnut litter may have allelopathic properties that limit the development of some common competitors in the southern Appalachians, including eastern hemlock and rhododendron (*Rhododendron maximum* L.). Good (1968) found that chestnut leaf extracts (1.8 ounce leaf per 1 fluid ounce distilled water) inhibited the germination of eastern hemlock and significantly reduced shoot length of black birch, yellow birch (*Betula allegheniensis* Britton), tomato (*Lycopersicon esculentum* Mill.), and eastern hemlock in a laboratory bioassay; he also found that adding chopped chestnut leaf material (5 g dry weight) to germination pots significantly reduced root length of tomato and root, stem, and leaf biomass of black birch. Vandermast and others (2002) found that chestnut leaf extracts (0.04 ounces per 0.7 fluid ounces of distilled water) significantly reduced seed germination of lettuce (*Lactuca sativa* L.), rhododendron, and eastern hemlock and also reduced the length of radicles of germinating lettuce and rhododendron. Although these studies clearly demonstrate the allelopathic potential of American chestnut, the nature of these studies prevents extrapolation of the results to field conditions.

Damaging agents—American chestnut might be the most susceptible tree in the Eastern United States to damaging agents. The most widespread damaging agent to American chestnut is the chestnut blight. The fungus was originally believed to be a new species and was named *Diaportha parasitica*, but it was discovered that it likely came into the United States on imported Asian *Castanea* species. The fungus was renamed *Endothia parasitica*, and then *Cryphonectria parasitica*, and it is most commonly referred to as the chestnut blight fungus (Anagnostakis 1987, 1992).

Common symptoms of chestnut blight include the presence of mycelium arranged in buff-colored fans on the inner bark, sunken or raised cankers on the infected tree, the appearance of stromata (orange fruiting bodies) on the smooth bark surrounding cankers, the development of sprouts below cankers, and small, dying leaves and nuts on affected stems (Anagnostakis 1987, Gravatt 1925, Hawley and Hawes 1925). Disease symptoms also include yellowing or wilting leaves that tend to persist on the tree past leaf abscission in autumn (Griffin and Elkins 1986). Cankers are usually found at the base of the tree and usually have an elliptical shape, extending up and down the trunk. Old trees susceptible to blight typically produce sunken cankers, while more vigorous or blight resistant trees produce slightly swollen cankers (Gravatt 1925, Griffin 2000, Griffin and Elkins 1986). The bark over the injury is typically darker red in color than the surrounding bark, and exposed wood is often at the canker center (Griffin and Elkins 1986).

As an ascomycete, the fungus produces small reddish-brown fruiting bodies on the surface of cankers where two different types of spores are formed (Gravatt 1925). Short-lived conidia are summer spores exuded in sticky masses. After summer rains these spores stick to the feet of birds, insects, and mammals and are carried long distances to infect other trees (Burnham 1988, Hepting 1974). Ascopores are winter spores that are carried long distances by wind to infect other trees by entering at a wound or split in the bark, where they germinate and enter the inner bark, killing vital cells as they invade (Burnham 1988, Hepting 1974). American chestnut trees commonly have wounds and punctures caused by insects, woodpeckers, and natural bark cracks (Ashe 1911). The fungus enters through these bark wounds, where it grows and has a girdling effect on the cambium of the tree. Although the blight has effective dispersal mechanisms, humans helped the spread by shipping diseased nursery stock, carrying the fungus on chestnut wood, and transporting spores on clothing, shoes, and tools (Hepting 1974).

Although the chestnut blight has certainly had the greatest impact on American chestnut populations across the native range, the species is also susceptible to other damaging agents (Jacobs 2007). Records of dying chestnuts caused by the root rot fungus *Phytophthora cinnamomi* can be traced back to 1824 (Crandall and others 1945). Woods (1953) reported that an epidemic of *P. cinnamomi* in the southern portion of the United States nearly eliminated chestnut from that part of its range from 1825–75. Crandall and others (1945) attributed *P. cinnamomi* to the disappearance of chestnut from the Gulf and Atlantic States as well as the foothills and mountains of Mississippi, Alabama, Georgia, Tennessee, Maryland, Virginia, North Carolina, and South Carolina. Ashe (1911) reported declining populations of chestnut throughout lower elevations of the Appalachians in Tennessee, and although not recognized at the time, the probable cause was *P. cinnamomi*.

This pathogen spreads primarily through free-moving soil water as zoospores that colonize fine-feeder roots; the fungus then can move into healthy cells of the main tap root and into the above-ground stem, forming lesions above the root collar (Crandall and others 1945, Robin and others 1992). Common symptoms of *P. cinnamomi* include sudden yellowing or wilt of the leaves during the growing season, followed by defoliation and death. The pathogen can also cause a gradual reduction in the size of the leaves over several years (Crandall and others 1945). Lesions of varying size with an ink-like exudate appear on the roots and root collar cankers, leading to the name "ink disease." The disease also affects red oaks, although it usually does not cause death (Robin and others 1992); however, it has been determined to cause the death of white oak and has been found in pine stands as well (Balci and others 2007, Campbell and Hendrix 1967).

Phytophthora cinnamomi is found in many forest types throughout the Southeastern United States (Campbell and Hendrix 1967, Hendrix and Campbell 1970, McLaughlin and others 2009) but is not tolerant of cold environments with annual minimum temperatures less than -20 °C (Balci and others 2007, Benson 2002). It is generally not found north of 40° latitude (Balci and others 2007) or in higher elevations at lower latitudes. In an experimental study with American chestnut seedlings, Rhoades and others (2003) found that the occurrence of *P. cinnamomi* infection was greater in wet soil than in dry soil, but around 25 percent of seedlings became infected regardless of soil moisture. Many observers noted the local decline and death of large numbers of American chestnut trees adjacent to one another, and such epidemics often began at poorly drained sites with heavy soils and then spread to higher, drier sites (Crandall and others 1945). However, susceptible trees on well-drained soils have also succumbed to the disease if the soil becomes infected (Balci and others 2007, Clark and others 2009, 2012a). Clark and others (2009, 2012a)[1] attributed failure in the first-year survival of pure American chestnut plantings in the Southeastern United States to *P. cinnamomi* that was probably brought in from nursery stock.

Phytophthora cinnamomi represents a large threat to restoration of American chestnut in the areas with climate and soil conditions favorable to the disease, including the Southern Piedmont, the Blue Ridge, and some areas within Tennessee and Kentucky. There currently exists no effective control of the disease in the nursery, in the field, or through breeding programs. Screening by the American Chestnut Foundation and the Connecticut Agriculture Experiment Station for resistance to the disease is in the beginning stages and shows promise (Anagnostakis 2002, James 2011, Jeffers and others 2009). The genes for resistance appear to be incompletely dominant but are different from genes controlling resistance in blight (Anagnostakis 2001). Therefore, it could be many years before trees resistant to both fungal pathogens are produced.

The Asian chestnut gall wasp (*Dryocosmus kuriphilus*) is a recently introduced pest that also poses a threat to American chestnut (Anagnostakis and others 2011, Jacobs

[1] Personal communication. 2011. Griffin, G.J. Professor Emeritus, Virginia Polytechnic and State University; and President, American Chestnut Cooperators Foundation, 2667 Forest Service Road 708, Newport, VA 24128.

2007). Introduced in Georgia in 1975, the species has quickly spread through the range of American chestnut and is now found throughout Tennessee and as far north as Cleveland, OH. Both American chestnut and Chinese chestnut are susceptible to Asian chestnut gall wasp, making it unclear how this species may affect chestnut hybrids developed for restoration (Anagnostakis and others 2011). The insect has been found on blight resistant hybrids planted in the field, but effects on seedling growth have not been yet determined.[2]

Other potentially harmful exotic pests include the Asiatic oak weevil (*Cyrtepistomus castaneus* Roelofs Coleoptera: Curculionidae), the gypsy moth (*Lymantria dispar* L. Lepidoptera: Lymnantriidae), and the Asian ambrosia beetles (Coleoptera: Scolytidae). The Asiatic oak weevil is an exotic pest from Japan that prefers to feed on species in the Fagaceae family, particularly oaks (Ferguson and others 1991, Frederick and Gering 2006). This species is especially damaging because larvae feed on roots and emerging radicles, while adults feed on leaves (Roling 1979, Triplehorn 1955). The Asiatic oak weevil was the most abundant insect caught in traps in a Missouri Ozark forest (Linit 1986) and is probably contributing to oak decline in those forests. The Asiatic oak weevil was found to be more prevalent on chestnut trees than oak trees, where it was found to completely defoliate young chestnut seedlings (Johnson 1956).

The gypsy moth is an exotic pest that was introduced from Europe, and the first gypsy moth outbreaks began around the same time as the chestnut blight fungus. The species has devastated vast areas of oak-dominated forests in the Appalachian Mountains in Virginia and northward through eastern deciduous forests. The gypsy moth could be a potential problem in defoliation of blight-resistant chestnuts, as it has been observed feeding aggressively on native chestnuts since 1915 (Mosher 1915). The gypsy moth was found to grow larger when fed leaves from second generation backcross chestnut hybrids when compared to leaves from pure American seedlings (Rieske and others 2003); similarly, gypsy moth grew better on transgenic chestnuts when compared to native American chestnuts (Post and Parry 2011). The preference of the moth for the BC_3F_3 generation of chestnut hybrid is currently unknown.

The Asian ambrosia beetles were first imported into eastern North America in the 1930s, and new species have recently been discovered (Atkinson and others 1990, Schiefer and Bright 2004). The insect bores into small saplings and trees, creating tunnels and galleries and potentially introducing fungi into the wounds. *Xylosandrus crassiusculus* Motschulsky has been found to negatively impact Chinese chestnuts in orchards in middle Tennessee (Oliver and Mannion 2001), but there is little information on effects these beetles will have on American chestnut seedlings, hybrid seedlings, or transgenic trees. Mortality caused by this insect was observed on the research plots of the American Chestnut Cooperators Foundation, typically on American chestnut stem < 4 in diameter.[3] Another recently imported Asian ambrosia beetle (*Xylosandrus mutilatus* Blandford) is known to be a pest to Chinese chestnut in its native China, but this beetle is currently south of the American chestnut species range (Scheifer and Bright 2004, Six and others 2009).

Two native insects that affect chestnut include the chestnut sawfly [*Craesus castaneae* Marshall Hymenoptera: Tenthrediniae] and the twolined chestnut borer (*Agrilus bilineatus* Weber. Coleoptera: Buprestidae). The chestnut sawfly feeds on leaves, and the only paper that has reported sawfly on chestnut showed that it was more damaging to trees planted in shaded environments than those planted in open conditions. In addition, the sawfly preferred hybrid (BC_2F_3) and American chestnut seedlings over Chinese chestnut seedlings (Pinchot and others 2011). The chestnut sawfly is a rare species and the impact of defoliation on chestnut restoration is unclear.

Historically, the American chestnut was the primary host of the twolined chestnut borer, but red oaks have become the primary host since the demise of chestnut (Haack and Acciavatti 1992). The insect is known to kill trees that are already stressed by first attacking the crown and then moving down into the trunk until the tree dies after 2–3 years (Cote and Allen 1980). The chestnut borer can invade after gypsy moth infestations, but populations can be reduced by removing dying trees and trees with poor vigor (Muzika and others 2000). No information exists on the impact this species will have on chestnut restoration, but the insect will likely only attack mature trees of low vigor.

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[2] Clark, S.L. 2012. The first research plantings of third-generation, third-backcross American chestnut (Castanea dentata) in the Southeastern United States. Manuscript in preparation. Proceedings from the 5th International Chestnut Symposium, Sheperdstown, WV, September 5-8, 2012. Author can be reached at 2431 Joe Johnson Drive, Room 274, Knoxville, TN 37996-4563.

[3] Griffin, S.L. 2011. Observations on ambrosia beetle damage. Unpublished data. On file with: American Chestnut Cooperators Foundation, 2667 Forest Service Road 708, Newport, VA 24128.

The effects of fire on American chestnut are not well understood. Some early observations report that chestnut is negatively affected by fire because of its thin bark and shallow root system, suggesting that anthropogenic fire in the Appalachian oak-chestnut forest may have limited natural chestnut regeneration (Ashe 1911, Buttrick and Holmes 1913, Paillet 2002, Russell 1987). Frothingham (1912) found that American chestnut was mostly absent from frequently burned forests of pitch pine and scrub oak. Fire damage to American chestnut bark may increase susceptibility to disease and insect infestation (Hawley and Hawes 1925, Russell 1987). However, the vigorous sprouting of American chestnut suggests that it may be able to persist following infrequent burning. Paillet (2002) noted evidence of fire preceding sharp increases in the proportion of American chestnut pollen in sediment. McEwan and others (2011) related patterns of fire frequency with changing forest composition from oak-chestnut forests to forests dominated by maple. To our knowledge, there exists only one experimental fire study using pure American chestnut seedlings to determine effects of fire on seedling sprouting and growth response, but this study is still in the early stages.[4] The complex interactions between site conditions, fire intensity, fire frequency, and fire season make it difficult to predict how American chestnut will respond to fire without additional research. However, the contrasting pattern of below- and above-ground biomass allocation between chestnut and oaks/hickories (Wang and others 2006) suggests that American chestnut may not be adapted to fire as well as oaks and hickories.

Extreme weather events, including excessive heating, low winter temperature, frost stress, and drought, may damage American chestnut. Excessive heating of the soil can injure chestnut when young (Hough 1878), and sprouts are sensitive to frost when green, tender, and close to the ground (Mattoon 1909, Zon 1904). The health and vigor of sprouts is impaired by excessive heat or cold (Zon 1904). Gurney and others (2011) reported that American chestnut saplings are approximately 5 °C less cold tolerant than red oak and sugar maple, suggesting that the northern limit of the range may be limited by cold tolerance.

SPECIAL USES

Perhaps the best known product of American chestnut has nothing to do with its wood value. The flavorful nut it produces was enjoyed raw, roasted, or boiled by Native Americans and settlers, and it was an important food source for livestock and wildlife such as turkeys and squirrels (Clapper and Gravatt 1943, Hepting 1974, Youngs 2000). For those living in the Appalachians, chestnuts were a supplemental food and provided a source of income, 60 cents to $5 per bushel (Zon 1904). During the late 19th century and early 20th century, chestnuts were a popular treat in large cities and could be a profitable small business venture.

American chestnut wood has a narrow whitish to light brown sapwood and grayish brown heartwood that darkens with age. American chestnut is an ideal tree for many common forest products because it is rot-resistant, straight-grained, and moderately light-weight, with an average specific gravity of 0.4. It experiences moderate shrinkage and has little tendency to warp or check when drying (Youngs 2000). In the past, American chestnut was used for heavy lumber, shingles, fuelwood, telegraph and telephone poles, rails, posts, pilings, trolley and railroad ties, and even musical instruments such as pianos (Hepting 1974, Smith 2000, Zon 1904). Frothingham (1912) reported that chestnut was used for building, bridge and car construction, interior finish, furniture, molding, and cabinet work, and because of its uniform density, American chestnut, was ideal for annealing brass, a process requiring good temperature control.

American chestnut was once the major source of tannins for leather production in the United States. With tannin content of 6 to 11 percent and numerous large logs available, American chestnut was an obvious choice for the tanning industry (Youngs 2000). Processed chestnut ended up in tanneries all over the Appalachians but also in Massachusetts, the leading leather-producing State. Dependence of the industry was such that even after most chestnuts were killed by the blight, dead trees were being harvested for tanneries (Clapper and Gravatt 1943).

GENETICS

American chestnut is thought to have the lowest genetic variability within the *Castanea* genus (Dane and others 2003, Huang and others 1998). The proportion of genetic diversity found among American chestnut populations is much lower than averages reported for species with a wide geographic range, species with any seed dispersal mechanism, species with similar modes of reproduction, or temperate species. Most genetic diversity appears to be within populations (Huang 1998). Low genetic diversity could be related to the demise of the species due to ink disease and chestnut blight.

[4] Clark, S.L. 2011. Thinning and burning effects on northern red oak and American chestnut. Manuscript in preparation. Author can be reached at 2431 Joe Johnson Drive, Room 274, Knoxville, TN 37996-4563.

American chestnut will readily hybridize with Chinese chestnut and Japanese (*Castanea crenata*) chestnut, crosses of which are being developed in search of a blight resistant tree (Anagnostakis 2002, Burnham and others 1986, Hebard 2005). A study by Clapper (1952) crossed American chestnut with Chinese, Japanese and Seguin (*Castanea seguinii*) chestnuts, as well as native chinquapin species, many of which have been more recently classified as varieties of *Castanea pumila*.

RESTORATION

Over the past 90 years, much research has been conducted to produce blight-resistant chestnuts using breeding techniques, biological control, and genetic engineering. Chestnuts were bred as early as the 1890s, primarily to improve nut production using hybrids of native chestnut and chinquapins with Asian and European varieties (Burnham and others 1986, Van Fleet 1914). Early breeding for blight resistance was first conducted in the 1920s by the Office of Forest Pathology, U.S. Department of Agriculture, and by Arthur Graves in his work with the Brooklyn Botanical Garden. Grave's work was later transferred in the 1940s to the Connecticut Agriculture Experiment Station (Burnham and others 1986). Early efforts were primarily focused on developing a single cross with the desired traits that could be vegetatively propagated (Diller and Clapper 1969, Graves 1942), but the programs failed by the 1960s primarily due to an inadequate understanding of inheritance of resistance and desired form (Burnham and others 1986). Alternative breeding programs have been attempted to develop crosses that promote natural resistance among existing American chestnut populations (Griffin 2000). Researchers with the American Chestnut Cooperators Foundation cross surviving American chestnuts, and have yielded a relatively high frequency of progeny with low levels of blight resistance (Griffin 2000). Since 1986, the American Chestnut Cooperators Foundation has planted over 135,000 trees of these progenies across the native range of American chestnut.

Hypovirulence of the chestnut blight has been tested as a means to control the disease (Anagnostakis 1982, Fulbright and others 1983, Jaynes and Elliston 1980). Research from Europe and the United States suggests that hypovirulent strains of the chestnut blight can weaken the pathogen (Anagnostakis 2001, Griffin and others 1983, MacDonald and Fulbright 1991). Hypovirulent strains of the blight can survive and spread for long periods in natural populations (Anagnostakis 2001). While widespread efforts to control the blight through hypovirulence alone are probably not realistic, biological control appears to be an important part of the solution (Anagnostakis 1987, Milgroom and Cortesi 2004).

Currently, the most promising option for widespread restoration of American chestnut is the development of a blight resistant chestnut variety through the backcross breeding programs of the American Chestnut Foundation and the Connecticut Agricultural Experiment Station (Anagnostakis 2002, Hebard 2005). The technique of using multiple backcrosses with the resistant parent did not begin until 1981. The breeding program includes the hybridization of American chestnut with Chinese chestnut or Japanese chestnut species that are naturally resistant to the blight. After the initial hybridization, subsequent back crossings with American chestnut progressively reduce the proportion of genetic material from the Asian parent, ultimately resulting in the third backcross hybrids (BC_3F_1) that are 94 percent American chestnut but retain the genes for blight resistance. After screen testing, BC_3F_1 hybrids that exhibit blight resistance are then intercrossed for two generations to create the BC_3F_3 hybrids, which retain 94 percent American chestnut genetics in progeny as well as high levels of blight resistance. The American Chestnut Foundation is currently in the testing phase of its BC_3F_3 seedlings through inoculations in controlled orchard settings. Early testing indicates that morphological traits of the BC_3F_3 hybrids are consistent with American chestnut (Diskin and others 2006), but more testing is needed to confirm that blight resistance will not break down as the trees age (Hebard 2005). The latest tests indicate the BC_3F_3 families are more resistant than the American parent but did not have as high of a blight resistance as Chinese chestnut. Selection is not yet complete in The American Chestnut Foundations' BC_3F_2 orchards.[5] The Forest Service, U.S. Department of Agriculture, also plants BC_3F_3 material in forest settings to test blight-resistance and morphological growth characteristics (Clark and others 2011, 2012a). Early results indicate that the BC_3F_3 generation has height growth similar to the American parent but bud break phenology that was slightly more developed than American chestnut (Clark and others 2011).

Genetic engineering of American chestnut is currently under way. Progress has been made in somatic embryogenesis to rapidly produce seedlings from multiple genotypes that have undergone genetic engineering using a wheat gene (Merkle and others 2007, Pijut and others 2011). The widespread deployment of genetically engineered trees on public lands will require addressing a number of ethical and social questions, as well as a relatively large funding

[5] Personal communication. 2011. F.V. Hebard. Data from Meadowview blight-resistance screening tests. Author can be reached at 29010 Hawthorne Dr., Meadowview, VA 24361-3349.

base (Merkle and others 2007). Deployment of trees bred using traditional breeding efforts is now under way (Clark and others 2011, 2012a) but selections of superior families are not yet complete. It is now understood that two or three incompletely dominant genes control blight resistance (Hebard 2005, Kubisiak and others 1997), and use of genetic marker-enhanced screening would speed up traditional breeding efforts substantially (Wheeler and Sederoff 2009). Candidate genes for resistance are currently being identified (Barakat and others 2009) that can later be used in biotechnology efforts to produce a blight-resistant tree or to assist in DNA-marker assisted selection. DNA-marker assisted selection is a promising technique that could refine the selection of traits in the traditional breeding programs, resulting in more efficient breeding and reducing the time required to develop resistance (Kubisiak and others 1997, Wheeler and Sederoff 2009). Therefore, it is possible that a large quantity of seeds of blight resistant American chestnut and American chestnut varieties could be produced in the near future for the purpose of restoration. Another critical need in American chestnut restoration is to test the durability of blight resistant American chestnut and American chestnut varieties developed by the American Chestnut Foundation and the American Chestnut Cooperators Foundation, especially under various environmental stresses that are known to affect the vigor of American chestnut (Griffin and others 2006).

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This report describes how the American chestnut (*Castanea dentata*) was ecologically extirpated due to an exotic pathogen, the chestnut blight (*Cryphonectria parasitica*), and describes current restoration efforts. The habitat, life history, special uses, and genetics of the American chestnut are detailed. The American chestnut was an important and versatile tree species until its demise from the chestnut blight. Backcross breeding techniques, the use of hypovirulent blight strains, and genetic engineering programs are currently being developed and tested to produce trees resistant to the blight fungus. The first putative blight-resistant trees have been planted and silvicultural techniques to improve competitive ability of chestnut are being tested. American chestnut is a fast-growing species with the ability to persist in shaded conditions, and responds favorably to forest management techniques that limit competition and increase available sunlight. Restoration will require advanced artificial regeneration techniques. The effects of damaging agents other than blight, including root rot caused by *Phytophthora cinnamomi*, Asiatic oak weevil (*Cyrtepistomus castaneus*), the gypsy moth (*Lymantria dispar*), and Asian ambrosia beetles (Coleoptera: Scolytidae) are not well understood, but may represent real barriers to restoration.

Keywords: American chestnut, backcross breeding, chestnut blight, exotic species, restoration, silvics, silviculture.

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